

The Role of Estuaries in the Development and Perpetuation of Commercial Shrimp Resources

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ABSTRACT

This report summarizes knowledge concerning functional relationships between the estuarine environment and commercial shrimp resources. Discussion is largely restricted to North American species; attention is focused upon situations evolving specifically as a result of the rapid urban and industrial development of our estuary-rich Gulf coast.

The association of shrimp and the brackish-water environment from ontogenetic and ecological points of view is reviewed. The question of continued productivity and perpetuation of shrimp stocks in the face of man's steady incursion of estuaries is considered. Also considered are measures that might be taken to counteract real, or imagined, effects of society's development of coastal wetlands.

INTRODUCTION

The broad, potential significance of the Nation's coastal swamplands, or "wastelands," as many have called them, was not recognized until fairly recently. Perhaps their first bounty, going back to the days of the early settlers, was realized in the form of furbearers, waterfowl, and fish—most of which still flourish in many of these areas. But it soon became apparent (Davis, 1956) that our vast estuaries offered much more: wetlands that could be rather easily "reclaimed" and then farmed, urbanized, or industrialized by an expanding society; ready-made cesspools for our manifold wastes; waters that could be deepened for waterborne transportation; underlying mineral deposits to extract; natural areas to develop for conflicting recreational uses; and freshwater inflow for diversion to municipal, industrial, and agricultural needs in regions of low rainfall. Such activities pose an ever-increasing threat to those creatures which collectively represent what should be viewed as a natural heritage to be carefully husbanded for food and fun in future generations.

It is unfortunate that in most instances we can only speculate about the possible demise of fishery resources seemingly dependent upon or inseparably linked to the estuary. Not the least of such resources are the stocks of shrimp of which our society is making relatively great demands, and upon which it consequently

places a high economic value. Just what is their relation to the estuarine environment? And, with man's steady incursion of our estuaries, what does the future hold for their perpetuation and continued productivity? Finally, what measures can be taken to offset the untoward effects of a rapidly progressing civilization?

At this point, it might be well to explain what is meant by the term "estuary." Webster's dictionary merely defines it as: "A passage where the tide (of the sea) meets the river current; especially, an arm of the sea at the lower end of a river . . ." In practice, as Ketchum (1953) points out, such a general definition does not sufficiently describe all estuaries. They range in diversity of configuration and character from the simple Scandinavian fjord to the extensive deltaic complexes at the mouths of large rivers like the Ganges, Amazon, and Mississippi. In between one can note the labyrinthine marshes that characterize the Chesapeake Bay area and lowlands of eastern New Jersey; the broad flats at the mouths of the Thames and the Elbe River in western Europe; the geologically interesting confines of San Francisco Bay; and the shallow-gradient Gulf coast of Texas and Louisiana that is a confusion of bays, rivers, creeks, bayous, and marsh.

To clarify, an estuary is neither the salt-water environment of the open sea, nor the freshwater environment of the river. It is a dynamic part of each, both the edge of the sea and the edge of the land; a buffer zone that is in a continual state of flux, being af-

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TABLE 1.—*United States imports of shrimp from various countries over the period 1950–64. Viewed serially, the data are intended to serve as rough indices of the degree to which shrimp fisheries are developing in different parts of the world*

[Millions of pounds, headless ¹]							
Country of origin	1950	1956	1960	1961	1962	1963	1964
British Guiana	—	—	3.6	3.5	4.1	5.5	5.5
Ecuador	—	3.0	4.2	4.7	5.1	5.6	5.8
El Salvador	—	—	6.7	8.1	7.2	6.7	6.3
India	—	1.0	2.9	3.2	5.6	9.9	10.2
Japan	0.1	2.6	2.9	1.8	3.9	4.1	2.9
Korea (South)	—	—	—	0.2	1.8	2.2	1.3
Mexico	39.7	53.7	73.6	79.2	77.7	76.5	72.1
Pakistan	—	—	1.0	1.7	3.2	3.7	4.8
Panama	0.1	5.8	8.4	9.9	10.1	10.3	12.1
Unspecified	0.3	2.5	10.1	14.0	22.5	27.0	33.6
Total imports	40.2	68.6	113.4	126.3	141.2	151.5	154.6
United States production	114.0	133.4	148.5	103.9	119.2	150.7	131.1
Ratio of imports to domestic production	1:2.8	1:1.9	1:1.3	1:0.8	1:0.8	1:1.0	1:0.8

¹ Import figures for 1960–64 are conservative since they include moderate quantities of fully processed shrimp (i.e., shrimp without heads as well as those cooked and with the “shell” removed), which were not converted to units of headless weight.

Source: Fisheries of the United States, 1961, 1962, 1963, and 1964. C.F.S. Nos. 2900, 3200, 3500, and 3800. Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service.

affected in varying degree by the sea, by the land, by the season, even by the hour of the day—as the ecologist would say, “an ecotone” in the truest sense of the word. From the above, the reader should encounter no difficulty visualizing throughout this report what is meant whenever the term “estuary” is employed.

To the continually changing environment so described there has become adapted an assemblage of many floral and faunal types. And within each estuary—simple or complex—there has developed accordingly a distinctive “ecosystem” composed of communities of biological elements exhibiting differential gradients of tolerance to each other as well as to an infinity of combinations of the physical and chemical factors that characterize it. From this ecosystem but a single constituent—the shrimp—has been selected for detailed discussion. The reader should strive at all times in the subsequent discourse to maintain in his thinking a contextual relationship between the shrimp and its associated fauna, particularly the fishes, molluscs, and other crustaceans.

IMPORTANCE OF THE NATION'S SHRIMP RESOURCES

Published fishery statistics quickly dispel any doubt as to the growing significance of shrimp in world trade (Table 1). Although these delicate crustaceans are viewed in most

quarters as strictly a luxury food item, exploitation of shrimp stocks has played (and still plays) no small role in furthering the national economies of countries the world over. Beginning well before the turn of the century, but not making appreciable strides until after World War II, development of the world's shrimp resources continues at an ever-increasing pace. So strong has the demand for shrimp products become that not only is utilization of hitherto unfished stocks being accelerated, but serious efforts are underway in many corners of the globe to increase shrimp supplies through artificial means.

Statistics also disclose that the United States ranks first in volume of shrimp landings (Table 2). The relative importance of domestic shrimp resources can be readily gauged by noting that annual harvests fairly consistently yield a greater aggregate income at the production level than do those of any other fishery resource (Figure 1). In summary, the United States is the world's foremost producer as well as importer and consumer of shrimp, and internal shrimp fisheries together with all other segments of the shrimp industry occupy a relatively prominent position in the American economy.

The most important of United States shrimp resources are those that occur on the Continental Shelf and in estuaries at the edge of the Gulf of Mexico. Stocks lying off the Atlantic and Pacific coasts jointly contribute,

TABLE 2.—*Annual landings of shrimps and prawns during the period 1960–62 by the major shrimp-producing countries of the world*
[Millions of pounds]

Country	1960	1961	1962	Average	Rank
Brazil	51.6	57.5	—	54.6	6
Germany (West)	52.9	59.1	53.1	55.0	5
India ¹	155.6	142.9	185.6	161.4	2
Japan ¹	133.6	162.0	174.8	156.8	3
Mexico	147.3	159.4	155.6	154.1	4
Netherlands	28.4	29.8	30.9	29.7	8
Spain	36.4	32.0	30.2	32.9	7
United States	249.4	174.5	191.1	205.0	1

¹ Figures for these countries also include very small amounts of other crustaceans.

Source: Yearbook of Fishery Statistics, 1962. Volume XV, Food and Agriculture Organization of the United Nations.

on the average, less than 20 percent to the total annual poundage of shrimp harvested by United States fishermen (Table 3). Year-to-year production in all areas is characterized by fluctuation of varying magnitude, explanations for which are currently being sought through State and Federal research programs.

During the first 4 years of the 1960's, commercial landings in Gulf of Mexico shrimp fisheries averaged slightly more than 171 million pounds worth about 56 million dollars to Gulf coast fishermen (U. S. Fish and Wildlife Service, 1962b, 1963b, 1964a). Roughly 17 percent of this volume originated in extraterritorial areas off the Mexican coast. The remaining 143 million pounds from United States waters is a conservative estimate because it does not include appreciable but unknown quantities taken for private use as food and bait.

Most shrimp taken commercially from the Gulf are stored and distributed in a frozen state, the remainder being canned, dried, or marketed fresh locally. In addition, increasingly large amounts are sold alive or dead as sport fishing bait (Inglis and Chin, 1959).

In general, the outlook for Gulf shrimp fisheries appears fairly good—provided, of course, that domestic stocks can be maintained at present or perhaps slightly higher levels. This observation does not imply, however, that Gulf shrimp fishermen will not be forced into a progressively more competitive position in the world shrimp market. At present domestic production contributes less than 50 percent to the total United States supply of shrimp (Table 1), with about four-fifths of this internal production—35 to 40 percent of

TABLE 3.—*United States landings of shrimp by region in various years from 1956 to 1964*
[Millions of pounds, whole]

Coastal region	1956	1958	1960	1962	1964
North Atlantic	—	—	0.1	0.4	0.9
South Atlantic	25.6	22.6	31.2	26.1	17.4
Gulf of Mexico	193.6	173.3	205.7	141.7	179.0
Pacific	5.0	17.9	12.4	22.9	11.0
Total	224.2	213.8	249.4	191.1	208.3

Source: Fishery Statistics of the United States, 1956, 1958, 1960, and 1962. Statistical Digests Nos. 43, 49, 53, and 56; also: Fisheries of the United States, 1964. C.F.S. No. 3800, Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service.

the total supply (1960–63)—originating in Gulf waters (Table 3). Prevailing opinion is that the major stocks of shrimp in the Gulf cannot be safely (or economically) fished to a greater degree than has been achieved in recent years. Consequently, only the development of presently unutilized species offers the Gulf coast shrimp industry any immediate prospects for expansion to meet the growing national demand for shrimp and shrimp products. Regardless of whether such expansion materializes, however, governmental agencies which share such responsibility can be expected to take whatever steps may prove necessary to protect all of the Gulf's shrimp resources from the adverse effects of man's activities, be they in the form of exploitation itself, or of gradual destruction of habitat.

ONTOGENETIC-ESTUARINE RELATIONSHIPS

For all practical purposes, we are concerned only with representatives of two groups of decapod Crustacea, namely, the caridean and penaeidean shrimps. Species of the Caridea, in which the female bears her eggs externally and the young hatch at a comparatively advanced stage of development, are of somewhat minor importance commercially, contributing on the order of 15 percent to the world catch of shrimp, and but 5 percent to United States landings. Penaeids (Family Penaeidae), in which the eggs are released directly into the water and hatch quickly into precocious young, are the real shrimps of world commerce, being usually in greater abundance, more readily accessible, of larger average size, and therefore of higher value.

In general, stocks of carid species support the shrimp fisheries of boreal seas. Prime examples are: (1) the deep-water fisheries

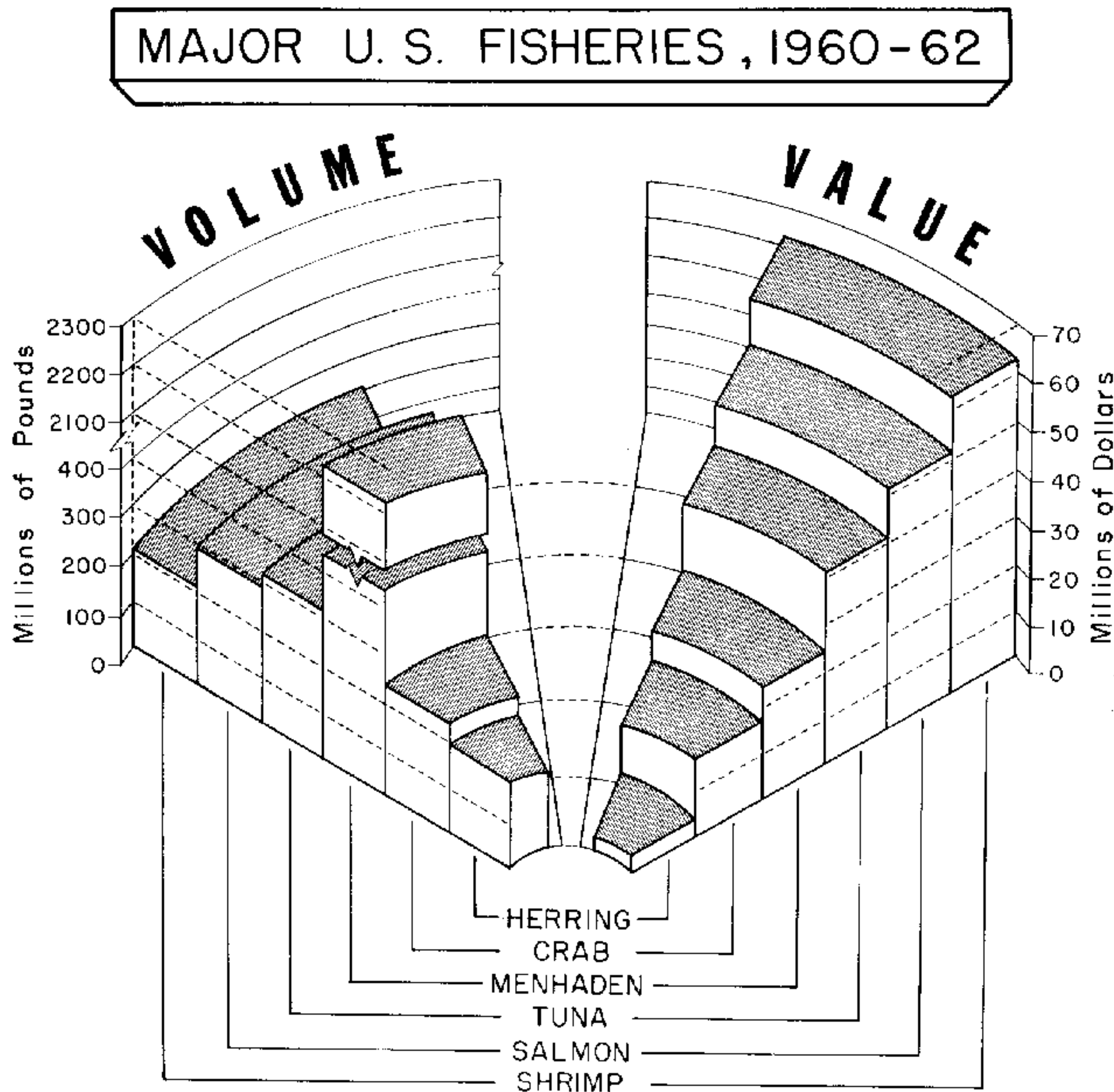


FIGURE 1.—Average annual volume and value of landings in major United States fisheries during the period 1960-62.

for *Pandalus borealis* in the North Atlantic off New England, Newfoundland, Greenland, and Scandinavia (e.g., Scattergood, 1952; Smidt, 1965), and for *P. jordani* off the Pacific coast of North America (Tegelberg and Smith, 1957), and (2) the shallow-water fisheries for *P. montagui* along the East-Anglican coast (Mistakidis, 1957), for *Crangon vulgaris* off western Europe (Tiews, 1954), and for *Crago franciscorum* in San Francisco Bay (Israel, 1936). Only in the biology of the latter three species do estuaries play an important role.

As a rule, the more prolific of the penaeid shrimps are closely associated with brackish, shallow-water environments. Upwards of 35 species, each with a different and somewhat restricted geographical distribution, support important coastal fisheries throughout the tropical and subtropical regions of the world. Isolated or overlapping stocks of these species are harvested commercially along the coasts of South America, Central America, Mexico,

southern Europe, and northern Africa; almost everywhere in the Indo-Pacific area and in Oceania; off China, Korea, and southern Japan; and along the Atlantic and Gulf coasts of the southeastern United States (e.g., Lindner, 1957; U. S. Fish and Wildlife Service, 1958a and b).

The penaeids of commercial significance occurring in the last-mentioned region include the brown shrimp, *Penaeus aztecus*; the white shrimp, *P. setiferus*; and the pink shrimp, *P. duorarum*. Brown shrimp stocks yield about three-fifths of the overall catch of shrimp, with the other two species contributing about one-fourth and one-seventh, respectively. Approximately the same proportions also hold for Gulf fisheries, which produce by far the bulk of shrimp taken commercially in all areas of the region (Table 3). No caridean species of value enter this catch.

Of particular interest from conservational as well as purely biological points of view

is the fact that most penaeid shrimps of commerce have a distinctive life history characterized by a period of more or less predictable length which is passed in an estuary or comparable brackish environment (see Weymouth, Lindner, and Anderson, 1933; Burkenroad, 1934, 1939; Pearson, 1939; Hudinaga, 1942; Williams, 1955; Hall, 1962). In each of the species so involved, the parent population, breeding in the sea at various distances from the mainland, produces seasonally large numbers of microscopic, semibuoyant eggs which almost immediately hatch into small, planktonic nauplii. Development proceeds rapidly through the protozoal and mysis stages, the larval shrimp all the while moving or being transported landward in a still-unexplained manner toward the mouths of rivers, or to passages into broad and shallow estuaries. The amount of time lapsing between hatching offshore and entry of the small shrimp into brackish waters inshore may vary from a few days to several weeks, again depending on the species as well as on prevailing oceanic conditions. In the case of Gulf of Mexico forms, namely, the brown, white, and pink shrimps, it is believed that usually 3 to 5 weeks have elapsed by the time the young begin to arrive in the bays as half-inch postlarvae, which no longer may be classed as true plankters. Once in the brackish water of estuaries, the postlarvae quickly transform into juveniles. Over the subsequent 2 to 4 months they grow rapidly and reach commercially acceptable size shortly before their return to the sea where the life cycle is completed.

Appreciable variation occurs among the commercial Penaeidae of the world, both in the degree to which each species utilizes an estuarine-type environment during its life history and in the distribution of its parent population along the brackish-marine gradient of the littoral zone at the sea's edge. Figure 2 illustrates how the more important penaeids generally differ from each other in these respects. The width of the spiral indicates the comparative length of time each new generation spends during early development in an estuary. A point on its axis represents the relative location of the species' parent con-

centration on the Continental Shelf along the environmental gradient from minimum "brackishness" and maximum fertility to true marine conditions. Information employed in the construction of this figure was drawn from various published sources.

Thus, a subspecies of the greasy-back prawn of eastern Australia, *Metapenaeus mastersii*, completes its life cycle wholly within the confines of an estuary (Morris and Bennett, 1951), while the scarlet prawn of the Atlantic Ocean (and Gulf of Mexico), *Plesiopenaeus edwardsianus*, undergoes entire development in the ocean at depths approaching 900 meters (Springer and Bullis, 1956; Maurin, 1965). In between may be noted all shades of difference in the ontogenetic-estuarine relationship. Fishable stocks of the valuable brown shrimp in the Gulf of Mexico, for example, reach maximum density some distance offshore (off the Louisiana-Texas coast) at depths of from 55 to 75 meters where most spawning occurs (Kutkuhn, 1962; U. S. Fish and Wildlife Service, 1963a). Accordingly, the young upon hatching have a fairly great distance to traverse before reaching the estuaries and, once there, remain only a comparatively short time (Figure 2). In contrast, adult white shrimp are rarely found at depths greater than 35 meters, well within that part of the littoral zone measurably influenced by land drainage. Their young not only spend more time in the estuaries, but penetrate them to a greater degree as well (Burkenroad, 1934; Lindner and Anderson, 1956). Similarly, the seabob, *Xiphopenaeus kroyeri*, a small species that in some years may contribute as much as 2 percent to the total United States harvest of Gulf shrimp (Kutkuhn, 1962), completes its life cycle within a very narrow zone lying against the coast. The young do not penetrate estuaries as deeply, nor do parent stocks concentrate as far offshore as their white shrimp counterparts (Burkenroad, 1934; Neiva and Wise, 1964).

The significance of the above information is best appreciated when one speculates on the fate of estuary-dependent shrimps in the event they are deprived of estuarine habitat. The basic question being asked by groups advocat-

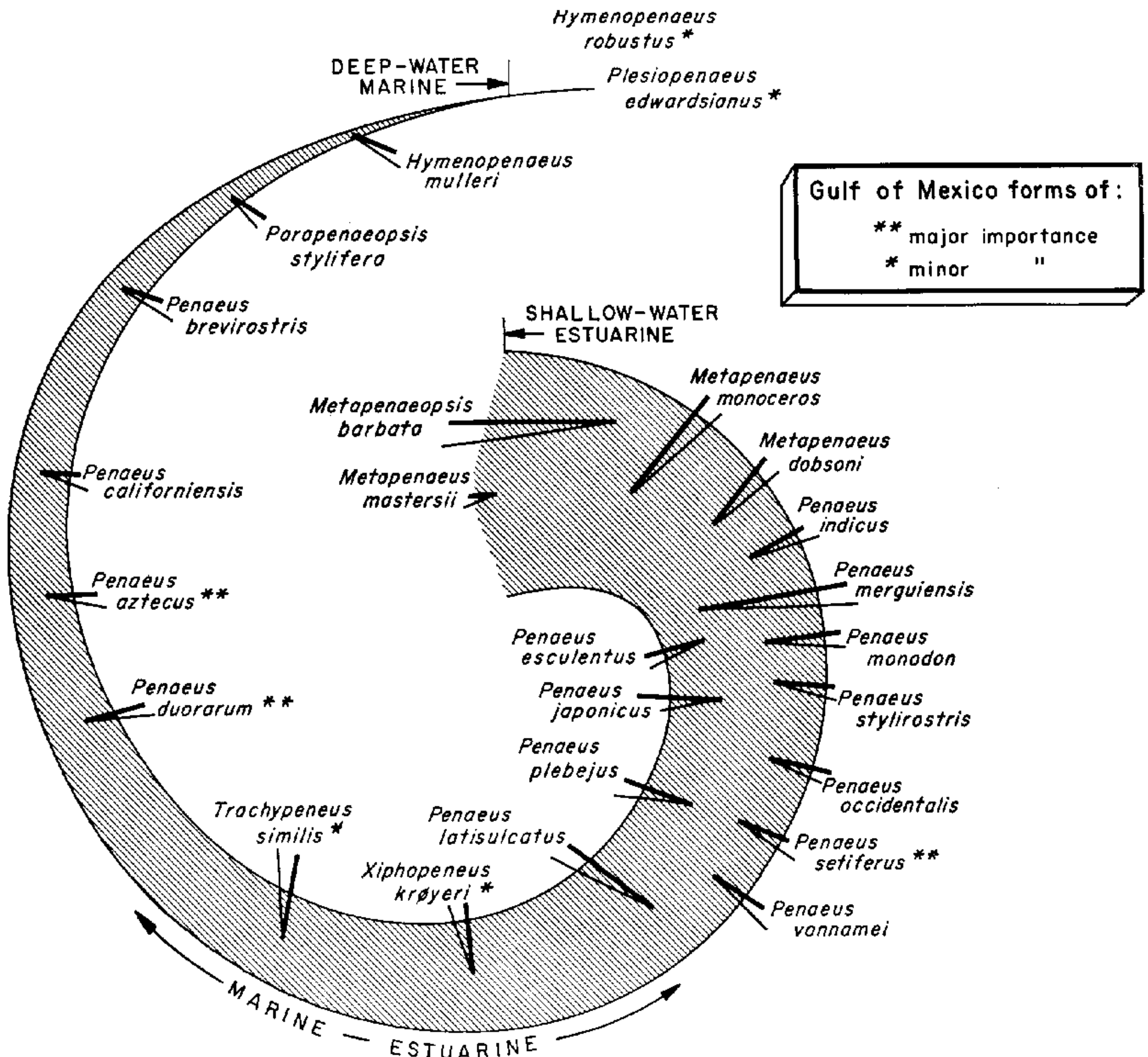


FIGURE 2.—Various penaeid shrimps of world commerce arranged arbitrarily in accordance with the expected degree to which each species inhabits an estuarine environment during its ontogenetic development. The relative position of each shrimp in the estuarine-marine spectrum was either based on the findings of specific life history studies, or inferred from scattered biological observations documented in numerous technical reports. (See text.)

ing development of estuarine areas at the probable expense of the living resources they contain is: Outside of complete reclamation of a system of estuarine basins, won't fishery resources such as shrimp adjust to the new conditions wrought by our activity? And, if not, why not?

Unfortunately, scientists are not yet in a position to answer either question satisfactorily. It stands to reason, from the material presented above, however, that any unusual

disturbance of the physical and chemical constitution of an estuarine system would almost certainly be manifested in subtle changes in each species' capacity to achieve a biomass equivalent to that attained under environmental conditions characterizing the ecological niche into which the species has evolved. Abrupt modification of their respective niches would, superficially speaking, affect every species to a different degree.

With the imminent erosion of the estuarine

biotope, the question of whether or not the more valuable species can adapt, overnight so to speak, to new combinations of environmental conditions considerably different from those experienced during their evolution is indeed a logical if not an urgent one. In the past certain species of value to mankind have adapted to what were first believed for them to be hostile environments. Others have gradually disappeared from the scene. Who's to say what will materialize in the case of shrimp? Majority opinion is that the fertile estuary, from the ontogenetic point of view, constitutes an irreplaceable factor in the survival strategy of major shrimp resources, and that the perpetuation of such resources *at commercial levels of productivity*, apart from their continued existence *per se*, will be contingent upon our ability to minimize disturbance of the shrimp's estuarine habitat.

Research by various agencies is slowly amplifying our knowledge of the biology and dynamics of shrimp resources at all stages of their life history. But much remains to be accomplished before we can muster the basic information that would provide an unassailable defense concerning the inadvisability of wholesale modification of vitally important coastal marshes.

THE ESTUARY AS SHRIMP HABITAT

The penaeid shrimps of commerce come and go in the manner described simply because that is the way they have evolved. What then typifies the highly dynamic environment occupied during the estuarine phase of their life history? We know when and where the young shrimp (late postlarvae, juveniles, and subadults) occur, and we can grossly describe their surroundings accordingly. But we fall far short of the mark in our ability to define even quasi-quantitatively the *functional* role of the environment.

What are believed to be the major factors regulating the occurrence and development of immature shrimp in the estuarine environment are, in a very general way, briefly described below. Complementing their description are limited discussions concerning present evaluation of cause-effect relationships, and the probable results of temporary as well as permanent changes in environment structure.

Environmental Factors and Biological Processes

Water circulation. Among the more important physical features of the estuarine-marine system are the wind-generated and tidal currents—Chapman (1960) regards the tidal cycle as the “master” factor—which play a large role in making the edge of the sea the highly variable and complex environment we observe it to be. Not only do currents constitute the principal mechanisms by which interchange of fresh and salt water is effected in the estuary (Ketchum, 1953), but the resulting circulation patterns also govern the distribution of: (1) other chemical components of the water in addition to salt content; (2) physical properties such as temperature; (3) suspended matter; and (4) biological populations, especially of those species whose early life history in the estuary entails one or more passive, planktonic stages.

Because of their very dynamic nature, circulation patterns in the estuary, let alone those on the Continental Shelf are not well understood and are therefore largely unpredictable. Much of the work accomplished in this area has been along theoretical lines with that reported by Ketchum (1951), Pritchard (1952a and b, 1955, 1959), proving particularly useful in studies concerning the ecology of estuarine resources.

The most significant advances in estuarine hydrology, from a practical standpoint, have been made by the U. S. Army Corps of Engineers through its extensive waterways experiment program. Procedure here consists of building accurate, small-scale models of specific estuarine basins and, on a trial-and-error basis involving simulated flow and exchange of fresh and salt water, determining how a change in basin configuration, the erection of a public works structure, or the introduction of pollutants will most likely affect an estuary's physical and chemical regimen. Successful models have included the San Francisco Bay (Calif.), Vermilion Bay (La.), Lake Pontchartrain (La.), Charleston Harbor (S.C.), Delaware Estuary, and Narragansett Bay (R.I.) systems. Agencies and persons, other than those interested solely in their engineering implications, have benefited from

the results of the many experiments conducted with such models (e.g., Pritchard, 1954). Fishery scientists especially have gained an understanding of the transport systems characterizing those estuaries and, as a consequence, are in a better position to prejudge how modification will affect, directly or indirectly, the productivity and general well-being of the valuable biological populations they influence (e.g., U. S. Fish and Wildlife Service, 1962a).

Current patterns on the Continental Shelf probably govern in large degree, ostensibly through distribution of the planktonic larvae during the oceanic phase of the shrimps' early life history, the eventual occurrence of post-larvae at the entrances to brackish-water nursery areas. To ascertain the role of ocean currents in the movement of young shrimp from offshore spawning grounds to inshore bays and marshes, the Bureau of Commercial Fisheries is now engaged in a broad, continuing survey of oceanic circulation in the northern Gulf of Mexico (U. S. Fish and Wildlife Service, 1963a and 1964b). Another investigation by the same agency is concerned with evaluating the effects of tidal currents as they facilitate or impede the movement of post-larvae into coastal wetlands. Throughout the young shrimps' occupancy of the estuary, however, there can be little question that circulation *per se* is the key process which, varying in pattern and degree from system to system, establishes indirectly the limits of environmental suitability in terms of temperature distribution, salinity, turbidity, nutrient levels, pollution, etc.

Temperature. Perhaps the pre-eminent environmental factor limiting productivity at all levels of the estuarine food chain is water temperature. Its importance in the case of Gulf coast shrimp resources is inferred from the simple observation that (despite evidence of measurable year-round spawning activity in some species) it is mainly just prior to or during the warmer months when the bulk of the larvae produced offshore enter the estuaries as postlarvae, and subsequent growth of the young shrimp in the bays is most rapid (e.g., Gunter, 1950; Lindner and Anderson, 1956; Baxter, 1963; St. Amant, Corkum, and

Broom, 1963; U. S. Fish and Wildlife Service, 1963a and 1964b). Overall, it appears that the situation in these months is generally conducive to the attainment of greatest biomass by a given generation of shrimp. But, to specify an optimum temperature range for the shrimps' brackish-water phase of development, as well as a quantitative measure of the expected long-term effects on shrimp populations of their exposure as postlarvae and juveniles to permanently altered temperatures is quite another matter.

At various stages during their sojourn in Gulf coast estuaries, the young of commercial penaeids have been observed at water temperatures ranging from near freezing to slightly above 95 F (U. S. Fish and Wildlife Service, unpublished data). At levels of 40 F and lower, mass narcosis and mortality frequently occur (Gunter and Hildebrand, 1951; U. S. Fish and Wildlife Service, 1964b). On the other hand, significant increases in shrimp biomass are not generally evident until the temperature reaches 70 F (St. Amant, Corkum, and Broom, 1963). Although the exact nature of their fate when exposed to high temperature is unknown, shrimp taken from waters exceeding 90 F are usually flaccid and highly sensitive to stresses induced by handling. Under extreme temperature conditions salinity and oxygen tension doubtlessly play important roles in controlling the survival of young shrimp.

Salinity and other chemical properties. One of its most variable yet easily measured attributes, salinity probably more so than any other property, characterizes the estuary (Pritchard, 1952). As implied earlier, it is something of a tribute to the penaeid shrimps and other forms similarly adapted that they have evolved with the capacity to endure wide ranges of salinity. Consequently they can take advantage at the most appropriate stages in their ontogeny of the high-nutrient reservoir represented by many estuaries. Other environmental features with which the shrimp are intimately associated while in the estuary—the quality and quantity of phanerogamic vegetation, for example (Chapman, 1960)—may be affected more by salinity differences than shrimp. Thus salinity is a property af-

fecting indirectly as well as directly the shrimps' well-being in estuarine nursery areas.

Penaeid shrimps, at one life history stage or another, have been observed in waters ranging in salinity from less than 1 (Gunter, 1956; 1961) to more than 60 parts per thousand (Gunter, Christmas, and Killebrew, 1964). Salinity optima for the young of commercial varieties found in estuaries along the United States Gulf coast are believed to vary from about 5 to 20 ppt (Gunter et al., 1964).

Much less is known about the spectra (as they relate to shrimp distribution, growth, and survival) of other chemical constituents distinguishing estuarine waters in which the polybiotopic shrimps are known to occur. Some data on dissolved oxygen, various nitrogen and phosphorus ions, vitamins, etc., may be found in the literature but they are so specific, scattered, or incomplete as to be either useless or meaningless. Perhaps the major reason for the sketchiness of such data is the highly ephemeral or capricious nature of many of these properties.

Pomeroy (1960), for example, attributes the very short residence time of dissolved phosphates to their rapid rate of turnover, which he notes is not only independent of but probably more important than phosphate concentration in maintaining good production in a given ecosystem. Similarly, Starr (1956) showed that detritus in water flowing from *Spartina* marsh immediately following high slack tide contained far more vitamin B₁₂, an important growth-promoting factor, than did detritus in water collected somewhat later in the same tidal cycle. These observations point up the general futility of taking anything other than the most systematic of measurements in attempts to establish cause-effect relationships between such properties and the biological populations they interactively control.

Turbidity and fertility. Also of great importance from a biological viewpoint is the relative degree to which the estuary's water column is penetrated by light. Obviously, the horizontal as well as vertical distribution of luminous energy in any body of water depends upon the quality, density, and areal extent of the suspended organic and inorganic matter it contains. Despite the consistently

large amounts of seston in many inshore areas, marked attenuation of light at any depth is rarely considered a factor impeding attainment of the high basic productivity typifying most estuaries, especially the very shallow ones bordering much of the Gulf of Mexico.

Still largely unresolved is the issue concerning the relative contribution of allochthonous materials and processes to the fertility of estuarine systems. Many elements (and biochemical mechanisms) collectively defining estuarine fertility may have their origin outside the estuary. Implying opposition to this opinion are statements by Odum (1961) and Schelske and Odum (1962) who, though recognizing estuaries as "nutrient traps," rank near the top of their list of factors responsible for high estuarine productivity: "... abundant supplies of nutrients . . ." which they maintain *are not* introduced through land drainage. Estuaries do serve as efficient "nutrient traps" through containment of dissolved and particulate matter by tidal action, but they also constitute basins in which nutrients and other essential elements are first entrapped and concentrated, and then promote through recycling the high productivity that distinguishes them.

The point is that estuaries are not closed, self-contained ecological systems. Their production of organic matter is as dependent on material contributed from land and sea as is their brackishness. The salt content of estuaries is regulated by the differential exchange of waters from the open sea on the one hand, and from extensive watersheds on the other, and so is their fertility controlled in large measure by allochthonous nutrients from the sea and, more importantly, from the land. Odum's (1961) views notwithstanding, there exists no tangible evidence that appreciable reduction in freshwater discharge and its "nutrient" load would not, in time, seriously impair estuarine fertility.

No successful studies have been conducted to relate turbidity with shrimp occurrence and density, but gross observation suggests that those bays which are consistently the most roily generally harbor per unit area and in season the largest concentrations of young shrimp. Whether this reflects more the nutritive potential of the detrital material in suspension, or

protection of transient shrimp from predation by fishes, birds, and other animals, remains a moot question. Results of investigations by Williams (1955), Flint (1956), Darnell (1958), and Hall (1962), among others, suggest that such material may serve in this dual capacity.

To the extent that the estuary's planktonic flora provides food for the young omnivorous shrimp, a gradual reduction of light at all levels of the water column, due, for example, to a steadily increasing silt load, could be expected to suppress algal productivity in open bay waters (Ragotzkie, 1959) and thereby indirectly inhibit the development of shrimp biomass. In most estuaries of interest here, however, it is highly improbable that such a decline in the algal food source would, by itself, significantly reduce their carrying capacity for shrimp.

Vegetation. Estuaries along the northern Gulf coast characteristically contain large amounts of suspended material and hence exhibit comparatively limited growth of submergents. Emergent vegetation on the other hand is usually well developed at the edge of bays, and especially so in their surrounding marshes. It is such areas—the shoreline zone and transitional marsh, typically vegetated with mangroves or with rushes, reeds, cane, and various grasses, particularly *Spartina* and *Distichlis*—that are sought by the young of most penaeid shrimps during the earliest stages of their estuarine existence, presumably for protection and food. Significantly, it is also the same areas which, through reduction of their vegetative cover due to chronically high salinity, would very likely be subject to gradual, widespread deterioration in the event freshwater inflow is decreased appreciably by one means or another (Chapman, 1960). The consensus of those investigating the biology of commercial penaeids is that the importance of the vegetated shore zone-marsh habitat surrounding most estuaries cannot be overemphasized.

Substratum. One other environmental factor meriting at least passing attention is the estuary's bottom structure as related to shrimp distribution. Repeated observations by fishermen have aroused speculation regarding its role in governing the carrying capacity of the com-

mercial shrimps' estuarine nursery grounds. But not until fairly recently has anyone attempted to demonstrate statistically that a relationship between bottom type and shrimp distribution may exist.

Williams (1958) showed by means of carefully designed laboratory experiments with the three major commercial species of the northwestern Atlantic and Gulf of Mexico, that the pink shrimp selected most often the comparatively hard substrate of mixed shell and sand; the brown and white shrimps occurred most frequently on softer bottoms composed of loose peat, sandy mud, or muddy sand. His experiments suggested that protective cover rather than food content was the primary attractant. From this limited information one may reasonably conceive that a gross change in substrate composition, arising, for example, from an increased silt load or a reversal in circulation pattern, with attendant changes in scouring action and rate of sediment deposition, could alter estuarine carrying capacity.

Response to Environmental Change

One finds it difficult to refute the conclusion that all the above factors, among a host of unspecified others, play complex interactive roles in determining the distribution, survival, and growth of young shrimp during their occupancy of the estuary. Yet, useful evidence of the mechanics involved, and of the extent to which changes in these factors influence the overall productiveness of commercial shrimp resources, is conspicuously lacking. So-called ecological investigations in numerous estuaries renowned as shrimp nursery areas have accomplished little more than detailed descriptions of the flora and fauna, and of the general features of the estuarine environment as a habitat for young shrimp. Apparently, specification of cause-effect relations between the brackish environment and the well-being of shrimp resources inhabiting it awaits the development of suitable mathematical and experimental techniques. The usefulness of such tools in furnishing guideposts so badly needed in the prejudgment of public works projects and other cultural activities that promise impairment of estuaries

and surrounding marshes may be readily envisioned.

Most research in the area of environment-induced stress on populations of shrimp has been performed through small-scale laboratory experimentation under simulated, carefully controlled conditions. Activity so far has ranged from attempts to explain the physiological mechanisms that permit young shrimp to adjust almost immediately to changes in salinity and temperature, to measurement of their general tolerance to temperature and salinity over a broad spectrum. Pannikar (1951) gives a useful introduction to the topic of regulatory capacity in estuarine-marine fauna (including penaeid shrimps), and its meaning from evolutionary as well as ontogenetic points of view.

In the case of physiological adaptation, Williams (1960) demonstrated experimentally that between 20 and 25 C the internal fluids of juvenile and subadult brown and pink shrimp have a lower osmotic pressure than the external medium when in ordinary sea water; they are hypertonic when the sea water is diluted to 30 ppt or less. He observed, too, that the shrimps' regulatory ability diminishes below 9 C, their blood tending toward isotonicity in the process. His findings also indicated that the pink shrimp is a better regulator at low temperatures than the brown shrimp, and that survival of both species under such conditions is probably best when the salinity is high. Similarly, McFarland and Lee (1963) concluded that subadults of brown shrimp and white shrimp adjusted their salt content hypo-osmotically in sea water, and hyperosmotically in a hyposaline environment. In contrast, stenohaline penaeids such as *Trachypeneus similis* and *Sicyonia brevirostris*, which ordinarily do not enter the estuary at any stage in their development, are slightly hypo-osmotic in sea water but succumb rapidly as salinity decreases.

Dobkin and Manning (1964), working with an estuarine and a freshwater species of the caridean genus *Palaemonetes*, determined that the estuarine form maintains constant osmotic concentration over a salinity range of 0.6 to 39.0 ppt, which indicates its blood is hypotonic

in a concentrated medium and hypertonic in a dilute medium. The freshwater form proved hypertonic over the range of salinity to which it is normally exposed, with its regulatory capacity breaking down at salinity levels in excess of 20 ppt. Broekema (1941) observed essentially the same characteristics in the common European shrimp, *Crangon crangon*, also a caridean species. In addition, he found that the difference in salt concentration between this shrimp's internal fluids and its environment increases with temperature.

Rao (1958) complemented these findings by demonstrating that oxygen consumption in *Metapenaeus monoceros*, a commercially important shrimp of the Indo-Pacific region, increased as the salinity of the experimental medium was reduced below that of the normal habitat. Two groups of shrimp were involved, one from brackish water, the other from the adjoining marine environment, and in each the percentage increase in oxygen consumption was clearly related to the osmotic difference between body fluids and test medium. Upon prolonged exposure to lowered salinity, however, the oxygen uptake gradually returned to "normal," indicating operation of a homeostatic mechanism actuated by osmotic stress.

Although they impart considerable understanding as to how polybiotopic shrimps adjust physiologically to a varying environment, these observations provide little more than a basis from which the effects on resource productivity of long-term upward or downward trends in temperature and salinity might be conjectured. Of current widespread interest is not so much an answer to the question of why and how these organisms can cope satisfactorily with their dynamic environment, but rather to what degree might the magnitude of their stocks be affected by permanent environmental changes.

Studies to resolve this question are underway at the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Texas. Bureau biologists have demonstrated that tolerance to salinity of postlarval and juvenile brown shrimp narrows perceptibly at reduced temperatures. Other findings provide evidence not only of the ability of young shrimp

to adapt readily to a broad spectrum of temperature-salinity conditions, but also of their ability to select suitable conditions so as to avoid osmotic situations involving undue physiological stress (U. S. Fish and Wildlife Service, 1963a and 1964b).

Experiments by Zein-Eldin (1963) indicate that rates of growth as well as survival in postlarval brown and white shrimp, with all other factors remaining constant, may not change significantly between salinities of 2 and 40 ppt. More recently, Zein-Eldin and Aldrich (1965) have confirmed the results of earlier growth and survival experiments in which brown shrimp postlarvae were shown to be capable of adjusting to a wide range of temperature-salinity conditions. They concluded, however, that higher levels of salinity are probably more favorable than lower ones as temperature limits are approached; growth, although good at all levels of salinity, is best within a somewhat narrow temperature range.

Of growing concern is our lack of information about the immediate or gradual fate of shrimp upon exposure during their estuarine phase to ever-increasing pollution. This offensive index of man's progress may be conveniently separated into three general categories on the basis of origin, namely, domestic, industrial, and agricultural.

Recent (unpublished) observations by Bureau of Commercial Fisheries personnel in Galveston Bay (Tex.) suggest that at least up to a certain level the presence of domestic wastes may be beneficial owing to the added fertility they bring to the environment. But explicit investigation of the effects of increased domestic pollution on concentrations of young shrimp in the estuary probably has not yet been attempted. Nor have the conceivable effects of chronic industrial and agricultural pollution been studied. Numerous laboratory experiments in which young shrimp were subjected to various dilutions of an industrial waste (Pulley, 1950), a mosquito-control chemical (Chin and Allen, 1958), and a variety of agricultural pesticides (U. S. Fish and Wildlife Service, 1959b, 1960, and 1961) suggest, however, that even at very low dilutions, many pollutants in these categories are lethal to shrimp. A major impediment to field

assessment of the true consequences of their prevalence in the estuary is our inability to identify and measure these toxic compounds (or perhaps their degradation products) with reasonable accuracy.

From the standpoint of the commercial shrimps' evolution and of their possible fate, the implications of preliminary information like that outlined above are fairly clear. Certainly, more research of this type is necessary, especially that treating other important environmental variables such as organic salts, turbidity, and food supply. Nevertheless, the work completed to date is providing needed direction for meaningful pursuit of ecological (cause-effect) relationships. The demand for information of this kind, with which to defend the maintenance of our estuaries as a necessary environment for biological resources of commercial and recreational importance, is becoming increasingly desperate. Consequently, attempts to translate even preliminary laboratory results into predictive techniques seem justified.

Natural Adversities

In the foregoing section attention was turned primarily to the general problem of forecasting the likely response of commercial shrimp resources to the very gradual or more subtle environmental changes that might be anticipated as an outgrowth of man's wholesale assault on the estuary. The development of mathematical models, employing ecological data which, in turn, are given direction by laboratory research was posed as a possible solution to this problem.

Not nearly so easily resolved are the consequences of unpredictable, largely infrequent, but often precipitant meteorological events. Included here are droughts, flooding due to heavy stream discharge, freezes, and tropical storms. The shallow estuaries and their biological populations are particularly prone to the effects of these occurrences. Unfortunately, only speculative information exists as to the real nature and extent of such effects. But it is evident that they would, in almost every case, be expressed initially in the abrupt change of one or more of the environmental properties discussed earlier.

Droughts. On the question of extended droughts and their relation to the annual productivity of commercial shrimp resources, the works of Hildebrand and Gunter (1953), Gunter and Hildebrand (1954), Parker (1955), and Viosca (1958) have perhaps stimulated the most thought. In each instance the species involved was the white shrimp which prior to 1948 constituted the mainstay of the Gulf coast shrimp industry. Whereas Viosca (op. cit.) merely conjectured the drought of the late 1940's and early 50's as being the principal cause for the sharp decline experienced by the white shrimp fishery of Louisiana and Texas during that period, the former two authors attempted a statistical correlation of annual white shrimp harvests with corresponding measures of precipitation. Their analyses suffered, however, due to inadequate fishery statistics and the inability to establish satisfactorily a functional relationship between resource productiveness and estuarine salinity.

Because of the young white shrimp's seemingly greater propensity for less brackish water than displayed by other species, it was assumed that higher estuarine salinities resulting from the drought caused environmental stress, reduced habitat carrying capacity, and therefore meant for this shrimp a lower annual biomass and yield. Such an assumption appears sound. But, as in the case of the shrimps' other environmental requirements, the salinity factor awaits experimental assessment in terms of its relative importance both alone and interactively with others.

Conversely, the sudden discharge into estuaries of greater-than-normal amounts of fresh water arising from heavy precipitation on upland watersheds could be viewed as beneficial. This was the position taken by Viosca (1938) who observed that the harvest of white shrimp from Lake Borgne and Mississippi Sound (La.) in 1937 (a year when a great volume of spring flood waters was diverted through the Bonnet Carre spillway into Lakes Pontchartrain and Borgne) exceeded the landings of any previous year. His rationale for this upsurge in shrimp abundance and fishing success paralleled that stated above, but it was tempered by the possibility of the increased amounts of nutrient

material carried by the flood waters into the estuaries.

Working in Australia with five penaeids similar in life history and habits to the Gulf of Mexico white shrimp, Thomson (1956) correlated their combined annual harvest and the amount of rainfall in various combinations of preceding units of time. He concluded on the basis of 17 years of observations in the Lake Illawarra region of New South Wales that: "The greater the rainfall of the previous two years the greater the prawn catch is likely to be." He did not venture an explanation of the mechanics involved.

So far as is known no other attempts have been made to demonstrate analytically the general effects of droughts and floods on the productivity of commercial shrimp resources.

Tropical storms. Even less attention has been directed toward evaluating the short-term but potentially disastrous influence of severe tropical storms on shrimp stocks. In ascribing causes of the sharp (55-percent) drop in the harvest of white shrimp from Louisiana waters in 1957, Kutkuhn (1962) considered the likely effects of two hurricanes, one of great intensity, which struck the Louisiana coast in late June and early August, respectively. The reasoning provided is as follows:

"The occurrence of these storms coincided with periods of peak (estuarine) and near-shore concentrations of (1) migrating juveniles representing the 1956 late-season brood, and (2) late postlarvae and juveniles representing the 1957 early-season brood. Although the mechanics involved are obscure, it is conceivable that factors such as: extended periods of high salinity, destruction of cover and food supplies, and excessive turbulence, all induced by extraordinarily high tides, acted corporately to disperse and otherwise exert greater-than-normal mortality in white shrimp populations during vulnerable (estuarine) phases"

Freezes. Among the regions of the world harboring commercial shrimp resources, only along the Gulf and South Atlantic coasts do abnormally low temperatures in estuaries and nearshore waters possibly influence shrimp supplies. Two factors appear equally responsible for this recurring problem: (1) the

prevalence of sizable stocks of penaeid shrimps near upper latitudinal limits for the tropical and subtropical (littoral) Penaeidae, and (2) the unique geography of the coastal region involved, which leaves it exposed to the full impact of polar fronts that sweep from north to south across North America.

The occurrence and immediately observed results of many freezes along the Texas coast have been recorded (Gunter, 1952) but none has prompted more discussion than those of the freeze of January 1940. Upon this widespread, intense, and protracted cold spell was blamed the mass mortality in Texas of thousands of pounds of fishes and invertebrates, including some shrimps of commerce, although adverse effects in terms of subsequently reduced shrimp supplies and commercial harvests never became evident (Gunter, 1941 and 1945; Gunter and Hildebrand, 1951). Lindner and Anderson (1956) reported a virtual loss of the white shrimp resource along the South Carolina and Georgia coasts in 1940 due, presumably, to the same cold wave. An explanation for the apparent geographical variation in the consequences of this uniformly widespread freeze has never been set forth, but it is significant to note that its observed effects in the case of commercial shrimps were short-lived as attested by the Carolina-Georgia fishery's return to normal the following year.

The susceptibility of fauna in Gulf and South Atlantic estuaries to the harmful influence of freezes is logically attributed by Gunter and Hildebrand (1951) to a combination of factors, the most important of which are the shallowness of the water, hence its capacity to cool quickly with the sudden passage of a cold front, and the restricted openings of many bays and bayous that impede the egress of organisms to avoid the rapidly dropping temperatures.

Modification by Man

If basic relationships between the physico-chemical features of the estuarine environment and the well-being of its biological resources are poorly understood to begin with, then it follows that we can neither fully appreciate nor predict the overall impact of permanent

changes in these features due to man's cultural activities. Although a moderate amount of information has accumulated on the local effects of public works and industrial engineering projects in terms of their physical and chemical alteration of coastal wetlands (e.g., Bourn and Cottam, 1950; Reid, 1956, 1957; Hutton, Eldred, Woodburn, and Ingle, 1956; and Rounsefell, 1964), nothing is known with any degree of certainty about the results of such alteration in terms of changed potential in shrimp and many other estuarine fishery resources.

At the present stage in the development of our knowledge on these matters, we are able merely to describe the general nature of proposed modifications, and to speculate on how they will be (or have been) reflected in the altered productivity of commercial shrimp resources. To save space and unnecessary discussion, I have accomplished these tasks in Table 4, which is self-explanatory.

By way of clarification, it should be pointed out that many of the features listed in Table 4 are interrelated. For example, the dredging of navigation channels, while greatly deepening a limited acreage of a particular bay system, often results in the deposition of spoil banks which may effectively subdivide the system in such a way that subsequent changes in shoaling patterns will render the segmented portions shallower and less useful as nursery area than previously. One may logically reason also that nearly every physical development of the estuary is aimed at enhancing the region involved for purposes of industrialization, urbanization, and other cultural pursuits, all of which can be expected to contribute ultimately, unless checked at the outset, to a pollution problem of enormous proportions and uncertain consequences.

Reference to Table 4 will also indicate the number and magnitude of engineering projects already completed or planned for Gulf coast estuaries. It is doubtful if comparable development of estuarine areas in other shrimp-producing regions of the world exceeds that in the southern United States.

In summary, most of man's engineering activity in coastal lowlands generally affects the estuarine shrimp habitat in two major ways: (1) change in mean salt content and

TABLE 4.—*Various types and likely consequences of man-induced modifications of the estuarine environment as a habitat for the young of economically important shrimps*

Feature	Examples	Expected environmental effects	Probable results in terms of resource productivity	
			Adverse	Beneficial
I. <i>Change in basin configuration:</i>				
Bulkheading and filling	Tierra Verde project (Florida); numerous bayside real estate developments (Gulf coast)	General reduction in acreage of desirable shore-zone and marsh habitat; alteration of marsh drainage patterns (e.g., Hutton, Eldred, Woodburn, and Ingle, 1956)	Decreased productivity due to loss of carrying capacity through destruction of plant cover and food sources	None
Dredging of navigation channels and "fish" passes	Intracoastal Waterway (Atlantic and Gulf coasts); Houston Ship Channel (Texas); Mississippi River-Gulf Outlet (Louisiana); Rollover Pass (Texas)	Partial deepening of bays; alteration of marsh drainage patterns; increased exchange of oceanic, bay, and marsh water; change in circulation and hence distribution of salinity, temperature, etc.; temporary increase in silt load (Rounsefell, 1964; Reid, 1956, 1957)	Possible intrusion of greater-than-normal amounts of sea water could decrease carrying capacity of marshes through reduction of plant cover and food sources	Increased carrying capacity through provision of access for small shrimp to previously inaccessible estuarine and marsh areas; deepened areas offer haven or routes of escape from effects of sudden cold fronts
Segmentation by spoil banks as well as by rail- and highway grades	Galveston Bay (Texas); Calcasieu Lake (Louisiana); Tampa Bay (Florida)	Lessening of average bay depth through shoaling due to structures' influence on circulation; reduced exchange of fresh and salt water (U. S. Fish and Wildlife Service, 1963a and 1964b)	Slight loss of bottom acreage, disruption of flow patterns, and impedance of shrimp movements would have nominal effect on productivity	None
Ditching of marshes	Maine to Georgia (Atlantic coast)	Lowered water table; gross change in vegetative cover; loss of nutrient material from marsh areas (Bourn and Cottam, 1950)	Loss in productive potential attributable not only to loss of plant cover and food sources, but to reduction in nursery acreage as well	None
II. <i>Protective works:</i>				
Stream-diversion spillways	Bonnet Carre spillway (Louisiana)	Redistribution of freshwater discharge; change in estuarine salinity regimen (Viosca, 1938; U. S. Fish and Wildlife Service, 1959a)	Depending on species, lowered carrying capacity in some areas	Depending on species, increased nursery acreage and hence carrying capacity in some areas
Salt-water barriers	Calcasieu Lake area (Louisiana)	Impeded exchange of fresh and salt water; altered patterns of salinity distribution	Limited reduction of carrying capacity due to loss of marsh habitat	None
Sea walls, dikes, and levees	Galveston Seawall (Texas); proposed hurricane-protection dikes (Texas) and closure of Vermilion Bay (Louisiana)	Restricted influx of salt water; loss of tidal-exchange benefits; change in salinity regimen (U. S. Army Corps of Engineers, 1959; U. S. Fish and Wildlife Service, 1962a)	Generally lowered productivity because of diminished access to broad estuarine areas for young shrimp	None
Tide-control structures	Lake Pontchartrain (Louisiana)	do.	do.	None

TABLE 4.—Continued

Feature	Examples	Expected environmental effects	Probable results in terms of resource productivity	
			Adverse	Beneficial
III. <i>Change in volume and seasonal distribution of freshwater inflow</i>	Numerous upstream dams (Gulf coast); proposed Texas Basins project (Texas)	Generally heightened salinity; increased concentration of downstream pollutants; reduced influx of terrigenous nutrient material (Chapman, 1966)	General deterioration of estuarine habitat, a vital link in the shrimps' survival strategy, would mean a measurable loss in productivity	None
IV. <i>Pollution:</i>				
Domestic	Galveston and Mobile Bays (Gulf coast); Thames and Elbe estuaries (Europe)	Change in water chemistry; increased biological demand for oxygen	Superenrichment could induce suffocation and loss of productivity	Increased fertility—limited enhancement of productivity
Industrial	do.	Change in water chemistry; presence of toxic or suffocating compounds	In cases of inadequate dilution, decreased shrimp survival and productivity	None
Agricultural (including mosquito-control measures)	Areas producing rice, sugar cane, and cotton (Gulf coast)	Introduction through sheet run-off of pesticides and herbicides (Butler and Springer, 1963)	do.	None
V. <i>Development of mineral resources:</i>				
Oil production	Louisiana and Texas (Gulf coast)	Ordinarily slight pollution; segmentation of bays by pipelines (see Item I)	Nominally decreased productivity due to somewhat poorer survival; hindrance to harvest of shrimp most significant result	None
Dredging of fossil shell deposits	do.	Change in bay circulation patterns; increased silt load	Some reduction of bay carrying capacity due to localized loss of shelter and feeding areas	Questionable

chemical composition, and (2) net loss of carrying capacity, particularly through loss of vegetated marshes as contrasted to open bay waters. It is highly problematical whether the estuary-dependent shrimps of commerce can adjust to such modification and still maintain their stocks at economic levels of productivity.

Aquiculture—"Shrimp Farming"

The culture of shrimps on a commercial scale is receiving wide attention in the United States and in several other countries. The process entails vastly improving the carrying capacity of a comparatively small area of estuarine habitat through manipulation of the numbers of young shrimp involved and the tight control of their biological and, to some degree, their physical environment. Most successful attempts at shrimp farming, whether subsistence fisheries such as exist in certain parts of South America (Allsopp, 1960) and throughout the Indo-Pacific (Hall, 1962), or commercial enterprises like the one being developed in Japan (Fujinaga, 1963), depend primarily on local tides of sufficient height to permit alternate flooding and draining of diked-off areas of swamp or bay. Of nearly equivalent importance are the adaptability to culture of local shrimp species, and the availability of young (seed) shrimp with which to stock the seminatural ponds at the beginning of each growing season. Descriptions of the many facets of shrimp culture as it is practiced in various parts of the world are given by Hudinaga (1942), Delmendo and Rabanal (1956), Kesteven and Job (1958), and Allen (1963).

To date, shrimp culture attempts in the United States have generally met with failure. One or more of the major reasons have been lack of adequate tide differential, difficulty in leasing or acquiring title to submerged lands, and the doubtful capacity of domestic shrimps to develop in quantity to profitable size under seminatural estuarine conditions (Johnson and Fielding, 1956; Lunz, 1956, 1958; Manning, 1963, 1964). Stimulated by ever-increasing interest in the apparent potential of such an industry, however, research on the biological and economic feasibility of shrimp farming in the extensive

tidelands of the southeastern United States promises to expand significantly over the next several years. On the basis of work already completed, it appears most likely that the white shrimp will prove the most amenable to commercial culture.

ESTUARINE RESEARCH: FAILURES AND PROMISES

In the preceding sections I have tried to describe what many believe to be the chief ecological factors controlling the growth and survival of valuable shrimp resources in the estuary. Attempts to rank these factors according to their relative importance, and to specify quantitatively their relation to the overall productivity of fishery stocks of interest, were thwarted at the outset, however, by the fact that such information is practically nonexistent. This handicap comes forcefully home to rest whenever fishery administrators or "experts" are faced with the task of pre-judging the effects of various cultural changes in estuaries on shrimp and other biological resources.

There is certainly no intent on the part of any conservation agency to stand in the way of progress. On the contrary, such groups are discharging with ever-increasing success their responsibilities to specify—even though in many cases on somewhat shaky grounds—the most probable effects of tideland development, so that steps can be taken to mitigate them through modification of project plans *before* construction begins and irrevocable damage to biological populations occurs. But despite improved cooperation from construction agencies, brought about through public opinion created by a growing realization that valuable natural resources are indeed being threatened, it still remains for us to elucidate the cause-effect relations upon which the conservationist's real defense of these resources must ultimately rest. This observation raises the fundamental question: In our investigation of the estuarine ecosystem, do we have the "problem" areas properly circumscribed and, accordingly, our objectives clearly in mind?

The kind and amount of estuarine research now being performed range from very restricted and basic inquiries on energy flow,

sponsored primarily by private institutions, to much broader ecological-hydrographical studies conducted mainly by governmental organizations for the purpose of providing information ostensibly having practical and immediate application. All such activities can be expected to yield results that in one way or another will enrich our knowledge of the estuarine environment and its inhabitants.

But, to what degree do (or will) the results of current work help resolve the grave issue at hand, namely, the unabated deterioration of estuarine habitat by a rapidly advancing civilization? Evidently very little. In many areas, especially in the shrimp-producing areas of the southeastern United States, the carefully planned assault continues, not because the construction agencies deny any appreciation for the multimillion-dollar commercial and recreational fisheries involved, but because conservation officials have not been able to defend in quantitative terms their arguments that engineering projects promise eventually to wreak havoc with these resources. All such projects are predicated on favorable benefit-cost ratios. It therefore follows that unless more tangible (and not necessarily totally unequivocal) testimony in behalf of the estuaries' important biological resources can be produced, the actual net benefits of any project cannot be properly determined.

If it could be stated with some mathematical certainty, for example, that the erection of a particular protective works would create a situation of chronically high salinity, and that over the years this condition in turn would result in a specified annual decline in production from the coastal fisheries affected, then the amount of monetary loss projected might be sufficient to render the benefit-cost ratio unfavorable and thereby impede development of the project, or at least force its redirection. The present-day fishery administrator rarely, if ever, finds himself in such a tenable position.

The difficulty seems to lie not so much in our basic approach to the problem at hand but in our inability to develop the analytical tools to resolve it. The synoptic ecological survey in the field, complemented by controlled experimentation in the laboratory,

would appear not only logically sound but realistic and intuitively correct as well. Awaiting the theoretician's skills, however, is the evolvment of autoregression, serial correlation, or other computer-oriented techniques without which the fishery scientist cannot synthesize quantitatively the multitude of concurrent biological, physical, and chemical data he is so carefully accumulating in many areas (Watt, 1964). For populations of shrimp and other transitory estuarine forms, an important prerequisite to such synthesis is a suitable index of net loss or gain in their biomass during the period they occupy the estuary. Statistical comparison of time-series of such a variable with corresponding series of environmental factors, singly and in combination, represents one way in which vitally needed information can be obtained. The sustained pursuit of somewhat unrelated investigations (e.g., the "pure" and, in many cases, vaguely directed research on primary productivity in the estuary) by public-supported agencies endowed with the initial responsibility of protecting fishery resources and their habitat appears questionable at this point. The fact remains that the estuarine environment is being changed drastically at an alarming rate, and unless all available and potential support—from research findings to public opinion—can be rallied to check it, anticipated encroachment threatens to nullify the estuary, not only as the producer of desirable food products and the site for a wide variety of recreational activities, but also as the object of scientific curiosity.

In conclusion, current government-sponsored research on shrimp, though rather limited in scale, has as one of its major objectives a working understanding of the functional relation between the shrimp and the collective facets of its estuarine habitat. Unfortunately, progress has been painfully slow and the point has barely been reached where we can say: "We've proceeded far enough descriptively, now let's get on with the analysis of function." For it is solely in the latter area, as sophisticated and costly as our approach may have to be, that our only real defense in insisting upon the perpetuation of our coastal fishery resources can be found.

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